

$$P = p_o r_o / \sin \beta, \quad \tan k\beta = 1/(\operatorname{ctn} k\alpha - \tan kl), \quad \tan k\alpha = kr_o.$$

I enclose the following errata in my article on horns cited above:

PAGE	EQUATION	FOR	READ
276	4	$\frac{k}{2V}i$	$\frac{k}{2\pi}i$
277	13	$uv$	$uv$
278	17	$uv, \alpha v$	$uv, \alpha v$
278	19-20	$d$	$\partial$
281	above 36	$Z_1 = ck^2\{$	$Z_1 = ek^2\{$
281	after 37	$H.K.$	$H.F.$
282		$\frac{d^2p}{vn^2} + m \frac{dp}{vn} + p = 0,$	$\frac{\partial^2 p}{\partial x^2} - m \frac{\partial p}{\partial x} + k^2 a = 0$
		$p = e^{-\sqrt{4-k^2}x} [A \cos kx + B \sin kx]$	$p = e^{\frac{mx}{2}} \{ A \cos k\sqrt{1-(m/2k)^2}x$ $+ B \sin k\sqrt{1-(m/2k)^2}x \}$
		$x = e^{-\sqrt{4-k^2}x} [C \cos kn + Dmkn]$	$X = e^{\frac{mx}{2}} \{ C \cos k\sqrt{1-(m/2k)^2}x$ $+ D \sin k\sqrt{1-(m/2k)^2}x \}$

### THE RELATIVE IMPORTANCE OF HEREDITY AND ENVIRONMENT IN DETERMINING THE PIEBALD PATTERN OF GUINEA-PIGS

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The Bureau of Animal Industry has been carrying on an experiment on the effects of inbreeding on guinea-pigs since 1906. Twenty-three families were started successfully from as many pairs and were maintained wholly by matings of brother with sister. Another stock from the same source has been maintained as a control, without mating even second cousins.

A number of color variations were present in the original stock and most of them kept appearing during the early history of each family as the result of Mendelian segregation. After a number of generations, however, a certain color became fixed automatically within each inbred line. In some cases an entire family came to produce only one color. In most cases, the families became broken into a number of sub-families, each characterized by a particular color.

The original stock consisted largely of tricolors. Conspicuous differences in the average amounts of white and yellow appeared among the inbred families from the first, proving the existence of hereditary differences in pattern. Contrary, however, to the case of the qualitative differences in color, no types of pattern ever became at all well fixed. Varia-

tions covering almost the entire range from solid color to solid white can be found in each line. Even after twenty generations of inbreeding, a guinea-pig with 20% of white in the coat may have a litter mate with as much as 90% of white.

As a supplement to more direct attempts to determine the cause of these variations in the pattern, it seemed desirable to find the relative importance of heredity and environmental factors.

The pattern of tricolors is really a combination of two patterns which are, in the main, inherited independently of each other, although obviously associated in development. These are the piebald pattern, consisting of colored spots on a white ground, and the tortoiseshell pattern consisting of black spots on a yellow ground. In a tricolor, a certain pattern of color and white is determined irrespective of the quality of the color. Another group of factors determines which spots shall be black (or one of the modifications of black, such as agouti, sepia or brown) and which shall be yellow or red.

A cross between a homozygous solid black and a tricolor of one of the inbred families produces black young with no yellow spots and only a very small amount of white, if any. On back-crossing with the tricolor stock, four kinds of young are produced in approximately equal numbers, viz., solid black, black and yellow tortoiseshells, black and white piebalds, and black, yellow and white tricolors. As in the first generation, there is apt to be a small amount of white in the first two classes. The nearly solid black type has been back-crossed for seven generations with pure tricolor stock, producing young with as much as 255/256 of the blood of the latter stock, with the same results as in the first back-cross, four classes of young in equal numbers. It is clear that two independent Mendelian factors are involved. One of the factors is completely dominant over that for tortoiseshell, the other is nearly but not quite fully dominant over that for piebald. In the stocks considered in the present paper both of these dominant factors were absent, leaving all of the animals tricolor except for the occasional somatic bicolors and black-eyed whites to be expected in a stock with a high average amount of white in the coat. The hereditary factors to be considered here, those by which one tricolor differs from another, are of the kind frequently known as modifiers. Crosses between inbred families at opposite extremes in amount of white have resulted in offspring which are almost exactly intermediate on the average. In the second generation, there is only a little more variability than in the first; much less than would be present if there were segregation of a single factor.

The minor as well as the major variations of the piebald and tortoiseshell patterns appear to be largely independent of each other, although at least one factor has been discovered which affects both, viz., sex. The males of all stocks have on the average some 7% more color than the females

and also some 4% more black within the colored spots. In the present paper only variations in the piebald pattern will be considered and the sexes will be dealt with separately.

A record of the patterns of the guinea-pigs has been kept from the first by drawing the spots within a rubber-stamp outline. Only as much of the pattern as is visible from the back was recorded in this way before 1915. Since that date, the patterns of both the back and belly have been recorded, but separately, making comparison with the earlier records possible. The amount of white in each case has been estimated by means of a piece of tracing cloth on which the area in the stamped outline is divided into ten equal dorsal parts and ten equal ventral parts, including the legs. Each guinea-pig is given a record such as B-R-W 2-5-3/X-5-5, meaning 20% black, 50% red and 30% white on the back, a trace of black, 50% red and 50% white on the belly. In the present paper only the dorsal areas are considered. As the correlation between the amount of white on the back and belly is 0.86 and the back contains the most persistent center of color (the ear region) and almost the most persistent white (the nose) the grades, based on the dorsal part only, are believed to be practically as satisfactory as grades based on the entire coat.

Figure I shows the distribution of grades of white in three of the inbred families and in the control stock in 1916 to 1918. The representatives of

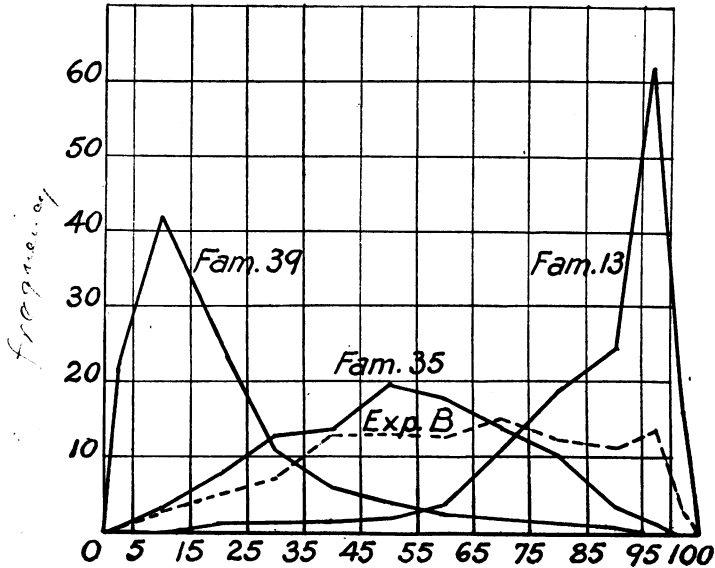


FIG. 1

Percentage distribution of grades of white in three inbred families (39, 35, 13) and in the control stock (B) during 1916-1918. The percentages with less than 5 per cent white and with 95 to 100 per cent white are given double value, the class ranges being of half size. The few solid whites in Family 13 and B are arbitrarily given double value.

family 39 during this period were all descended from a single mating in the fourth generation of inbreeding, and with a few exceptions, from one in the eighth. Family 35 was descended wholly from one mating in the seventh generation and largely from a single one in the twelfth. Family 13 was descended wholly from one mating in the second generation and largely from one in the seventh.

It will be seen that each family varies almost through the entire range, but that the mean values are markedly different. Family 39 has only about 20% white on the average, family 13 at the opposite extreme has about 85%, while family 35 has its average near 50%. On attempting to

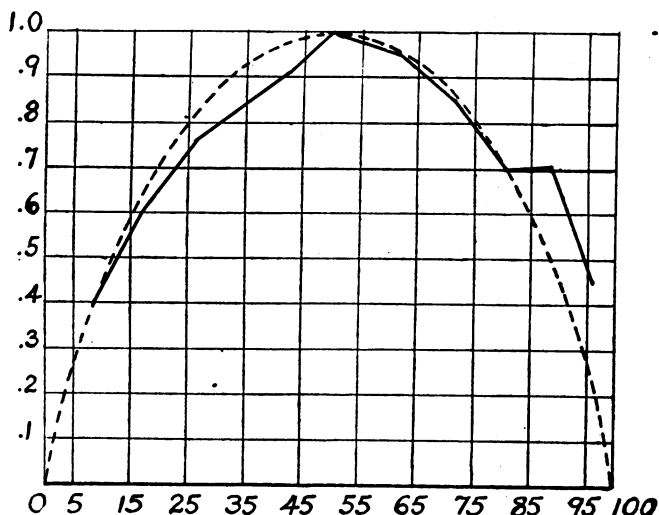


FIG. 2

The solid line shows the average distance between quartile and median in distribution curves from different inbred families in which the midpoint between quartile and median falls at different percentages of white. Based on 68 quartiles. The average quartile distance near 50 per cent white is taken as the unit. The broken line shows the expected quartile distances according to the hypothesis discussed in the text.

compare the variability of the families, a difficulty at once becomes apparent. The distribution curve of family 35 is practically symmetrical, but those of families 39 and 13 are markedly skew in opposite senses. This is not because of overstepping of the physiological limits, as there were no solid colored guinea-pigs in family 39, and only 8% black-eyed white in family 13. The curves appear to be compressed at the ends of the range, indicating that a unit of variation in these regions means more than in the middle of the range. It is especially difficult, so to speak, to remove the last bit of color, or the last bit of white. This phenomenon is shown by all of the stocks in which there is not an approximately equal average amount of color and white.

It is clear that measures of variability have little value unless the grades are properly corrected. Two methods have been tried for making this correction, one empirical, the other theoretical. The distribution of grades of white was tabulated, in males and females separately, in the 17 families which were still on hand during 1916 and 1917. With a properly corrected system of grades the variability should be approximately equal in all cases. The points were found which divided each distribution into four equal parts, i.e., the median and two quartiles. The distance between the median and each quartile was then correlated with the grade midway between the two points. The average of the values which fall within one grade is shown in the solid line in figure 2. It will be seen that a given variation near the middle of the range corresponds to one about half as great near the ends.

An effect of this kind is to be expected on theoretical grounds. Although the skin of a piebald guinea-pig is divided sharply into areas in which pig-

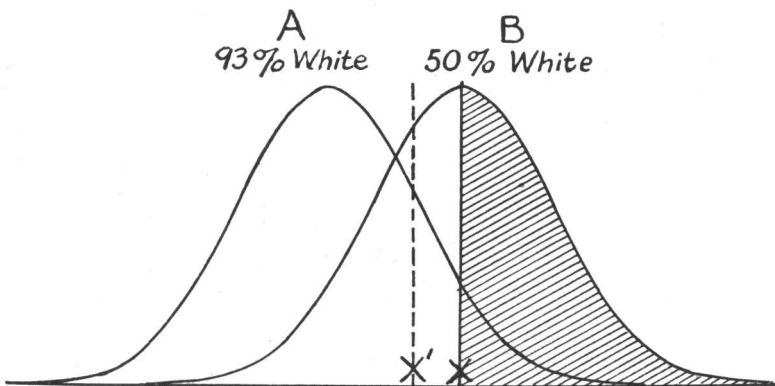


FIG. 3

The two curves are intended to represent the distribution of color potentialities among areas in the skins of two guinea-pigs.  $X$  is the critical potentiality, above which color is developed. The same change in average potentiality increases the amount of color in the guinea-pig with a large amount of white (A) only half as much as in the guinea-pig which is half white and half colored (B).

ment is either produced to the full amount characteristic of the animal, or is wholly absent, it is not to be supposed that the influences which at some critical period in ontogeny determine whether a region is to be colored or white, are so sharply alternative in themselves. It seems more reasonable to suppose that the sums of the favorable and unfavorable influences in different parts of the skin could be arranged in a graded series. Doubtless in certain white regions a slight difference in the conditions would have enabled color to develop, while in others, a great change would have been necessary. Similarly with colored areas. Suppose, then, that the skin is divided into a large number of equal areas and that it were possible

to determine the true potentiality of each area at the critical period in development. Let us assume that these potentialities are distributed, at least roughly, according to the normal probability curve.

In figure 3 variation in the piebald potentiality is measured along the horizontal axis. Curve *A* is intended to represent the number of areas with each potentiality in one guinea-pig, while curve *B* represents the same for another guinea-pig in which the tendency toward color production is higher as a whole. The critical potentiality is at *X*. All areas which exceed this produce color, while those which fall below, however slightly, remain white. Guinea-pig *A* is thus about 93% white, while *B* is about 50% white. It is easy to see that any cause which increases the potentiality

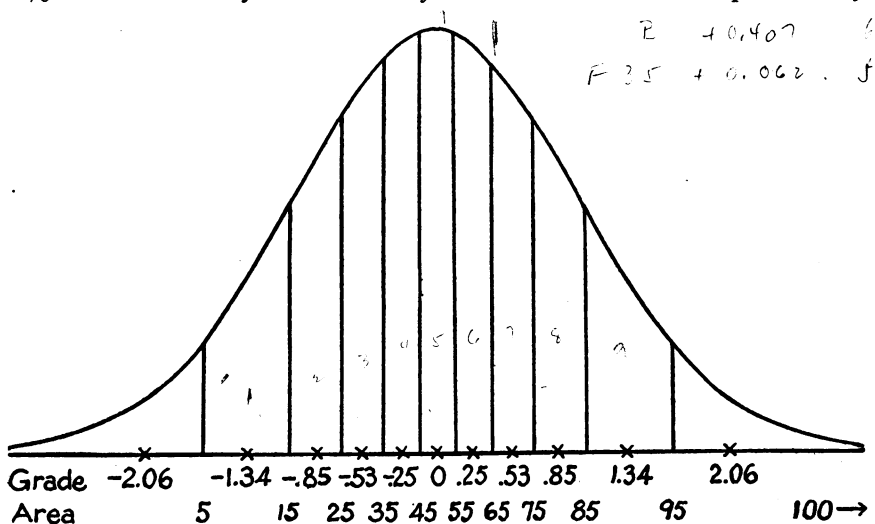


FIG. 4

A normal probability curve, the area of which is divided into tenths with the exception of the end areas which are twentieths. The deviations from the middle of the curve to the middle of each area (mean of the end areas), measured in terms of the standard deviation, are used as a corrected series of grades in place of the actual percentages of white in piebald guinea-pigs.

of *A* and *B* by a given amount makes a greater change in the area of color in *B* than in *A*. From a table of probability integrals, one can find at once the change in the area of the curve, brought about by a unit change in the value of *X*, in the neighborhood of any given area. These results should be comparable with those obtained empirically for physiologically equivalent variations at different areas of white.

The theoretical curve, as shown by the dotted line in figure 2, does not fit the empirical curve perfectly, but appears to give a sufficiently accurate correction of the grades for practical purposes. Aside from its greater smoothness, the theoretical curve has the advantage that by its use the variability in the amount of color in a stock of guinea-pigs can be compared

with the theoretical variability in the potentialities within a single average guinea-pig.

The relative importance of unit variations in area in different parts of the range is as the reciprocal of the variations which are physiologically equivalent. In figure 4 the area of a probability curve is divided into equal tenths except for the end areas, which are twentieths. The difference in potentiality corresponding to any difference in area can easily be estimated. The corrected series of grades as given in figure 4 has been made by finding the average of the deviations from the median of the curve to each of the class limits, with the exception that the deviation of the mean has been used for the end classes. A little consideration will show that the proper centering of the grades varies slightly with the mean of the population with which one is dealing. The grades as corrected here, are, however, sufficiently accurate for the present purpose.

TABLE 1

NUMBERS, MEANS AND STANDARD DEVIATIONS IN RANDOM-BRED STOCK AND INBRED FAMILY NO. 35 DURING 1916, 1917 AND 1918

	EXP. B (RANDOM-BRED)			FAMILY 35 (INBRED)		
	No.	Mean	$\sigma$	No.	Mean	$\sigma$
Sire.....	105	+0.337 $\pm$ 0.050	0.756 $\pm$ 0.035	73	-0.071 $\pm$ 0.044	0.559 $\pm$ 0.031
Dam.....	107	+0.390 $\pm$ 0.054	0.824 $\pm$ 0.038	73	+0.220 $\pm$ 0.045	0.570 $\pm$ 0.032
Son.....	498	+0.273 $\pm$ 0.024	0.808 $\pm$ 0.017	235	-0.017 $\pm$ 0.026	0.593 $\pm$ 0.019
Daughter	488	+0.543 $\pm$ 0.024	0.796 $\pm$ 0.017	236	+0.140 $\pm$ 0.027	0.613 $\pm$ 0.019
Total Offspring	986	+0.407 $\pm$ 0.017	0.802 $\pm$ 0.012	471	+0.062 $\pm$ 0.019	0.603 $\pm$ 0.013

Compare with figure 4 for conversion of grades into percentages of white. The standard deviation of 0.603 in the inbred family means about 22% of the total dorsal area of the coat.

Two stocks were chosen for study of the relative importance of heredity and environment. One of these was the control stock (*B*) in which matings were made at random, except that even the mating of second cousins was avoided. The other was family 35, which since 1915 has been descended entirely from a single mating in the seventh generation of inbreeding and largely from a single mating in the twelfth generation. The records for 1916, 1917 and 1918 were used in both cases. Table 1 gives the number in each experiment, the means and standard deviations. Table 2 gives the correlations between parent and offspring, between litter mates and between the parents, weighted by the number of young. Inspection of the tables shows that sex makes no significant difference in the correlations. This is in agreement with the results of direct experiments. Reciprocal crosses between inbred families at the opposite extremes, as families 39 and 13 in figure 1, produced practically the same result, the progeny in

both cases being almost exactly intermediate. Sex also makes no significant difference in variability. In the case of the means, however, there is in all cases the sex difference already mentioned. The mean and standard deviations are measured on a scale in which unity is the standard deviation of color potentialities for areas within the skin of a single average guinea-pig. It is interesting to find that even the random-bred guinea-pigs differ less among themselves in average color potentiality than do the separate skin areas of a single animal.

TABLE 2

CORRELATIONS BETWEEN PARENTS, BETWEEN PARENT AND OFFSPRING AND BETWEEN LITTER MATES IN RANDOM-BRED STOCK AND INBRED FAMILY NO. 35, DURING 1916, 1917 AND 1918

	EXPERIMENT B (RANDOM-BRED)		FAMILY 35 (INBRED)	
	No.	Correlation	No.	Correlation
Sire-Dam.....	105	+0.019 $\pm$ 0.066	73	+0.029 $\pm$ 0.079
Sire-Son.....	492	+0.231 $\pm$ 0.029	235	+0.013 $\pm$ 0.044
Sire-Daughter.....	484	+0.194 $\pm$ 0.030	236	+0.082 $\pm$ 0.044
Dam-Son.....	498	+0.251 $\pm$ 0.028	235	+0.042 $\pm$ 0.044
Dam-Daughter.....	488	+0.165 $\pm$ 0.030	236	-0.080 $\pm$ 0.044
Average, Parent-Offspring.....	1962	+0.211 $\pm$ 0.015	942	+0.014 $\pm$ 0.022
Brother-Brother.....	390	+0.219 $\pm$ 0.033	182	+0.090 $\pm$ 0.050
Brother-Sister.....	437	+0.228 $\pm$ 0.031	203	+0.062 $\pm$ 0.047
Sister-Sister.....	406	+0.180 $\pm$ 0.032	194	+0.064 $\pm$ 0.048
Average, Litter Mates.....	1233	+0.214 $\pm$ 0.018	579	+0.069 $\pm$ 0.028

The matings in the correlation between sire and dam are each weighted by the number of offspring. The probable errors in this case are based merely on the number of matings. The probable errors in the other cases are based on the number of entries in the tables. Owing to repetition of individuals, they are probably somewhat too small. The correlation between litter mates in experiment B is based on 894 individuals in litters in which two or more were graded. The probable error based on this number is  $\pm 0.022$  instead of  $\pm 0.018$  as given in the table. Similarly there were 426 individuals in such litters in family 35, giving a probable error of  $\pm 0.031$  instead of  $\pm 0.028$ .

The negligible correlations between the parents (+0.019 in the control stock and +0.029 in the inbred family) show that matings actually were made at random as far as color is concerned. In the control stock, both the average correlation between parent and offspring (+0.211) and that between litter mates (+0.214) are unquestionably significant. In the inbred family, there is virtually no correlation between parent and offspring (0.014) while that between litter mates is of doubtful significance (+0.069).

There is evidently very little genetic variability left in family 35, but is a good deal in the control stock. A closer analysis can be made by con-



sidering the relations between parent and offspring as shown diagrammatically in figure 5.

In a broad sense, the peculiarities of an individual are entirely determined by heredity and environment. In the present and doubtless most other cases, the latter should be divided into two elements. Nearly all tangible environmental conditions—feed, weather, health of dam, etc., are identical for litter mates. There may, indeed, be some differences in the blood supply, but in the main, differences which are not genetic must be due to irregularities in development due to the intangible sort of causes to which

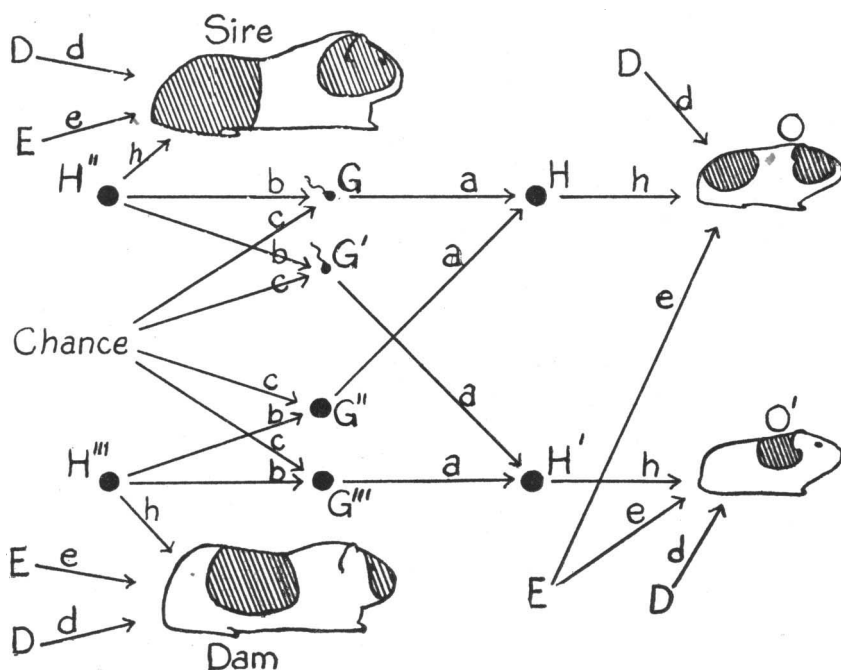


FIG. 5.

Diagram illustrating the casual relations between litter mates (O, O') and between each of them and their parents. H, H', H'', H''' represent the genetic constitutions of the four individuals, G, G', G'', and G''' that of four germ cells. E represents such environmental factors as are common to litter mates. D represents other factors, largely ontogenetic irregularity. The small letters stand for the various path coefficients.

the word chance is applied. Variations which are due to inaccuracy in grading and are, therefore, merely apparent, cannot, however, be distinguished from those of this class. Checks have been made which indicate that apparent variability due to this cause is small in comparison with the large amount of variability which is found to be due neither to heredity nor to tangible environmental conditions.

In the diagram, the pattern of each guinea-pig is represented as determined by three factors,  $H$  (heredity),  $E$  (environment common to litter mates before birth) and  $D$  (the residue, largely irregularity in development). Our problem is to determine the degree of determination by each of these factors.

In a forthcoming paper, a method of estimating the degree to which a given effect is determined by each of a number of causes will be discussed at some length.

Figure 6 is meant to illustrate a system in which the variations of two quantities  $X$  and  $Y$  are determined in part by independent causes, such as  $A$  and  $D$ , respectively, and in part by common causes such as  $B$  and  $C$ . These common causes may be correlated with each other as in the figure. It is assumed that all of the relations are approximately linear and that the influence of the various causes are combined approximately by addi-

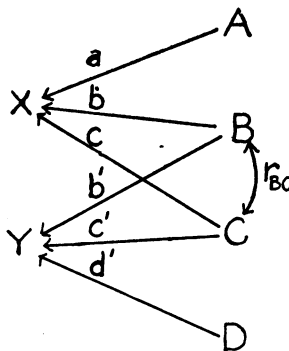


FIG. 6

Diagram illustrating two effects ( $XY$ ) which are determined in part by the same correlated causes ( $BC$ ).

tion. The path coefficient, measuring the importance of a given path of influence from cause to effect, is defined as the ratio of the variability of the effect to be found when all causes are constant except the one in question, the variability of which is kept unchanged, to the total variability. Variability is measured by the standard deviation. The path coefficients in the figure are represented by small letters.

It can be shown that the squares of the path coefficients measure the degree of determination by each cause. If the causes are independent of each other, the sum of the squared path coefficients is unity. If the causes are correlated, terms representing joint determination must be recognized. The complete determination of  $X$  in figure 6 by factor  $A$  and the correlated factors  $B$  and  $C$ , can be expressed by the equation:

$$a^2 + b^2 + c^2 + 2bcr_{BC} = 1 \quad (1)$$

The squared path coefficients and the expressions for joint determination measure the portion of the mean square deviation of the effect due to the causes singly and jointly, respectively.

The correlation between two variables can be shown to equal the sum of the products of the chains of path coefficients along all of the paths by which they are connected. In figure 6

$$r_{XY} = bb' + cc' + br_{BC}c' + cr_{BC}b'. \quad (2)$$

The path coefficients in a system of causes and effects can be calculated, if a sufficient number of simultaneous equations can be made, expressing the known correlations in terms of the unknown path coefficients as in the last equation (2), and expressing complete determination of the effects by their causes as in equation (1).

The correlation between characteristics of parent and offspring are represented in figure 5 as tracing back to a single cause, the genetic constitution of the parent. Litter mates on the other hand are correlated for three reasons, the genetic constitutions of the sire and dam, respectively, and the common environment. In the absence of assortative mating, these causes are not correlated with each other. In such a system, the path coefficients are merely coefficients of correlation.

That the square of the coefficient of correlation measures the degree of determination of one variable by another in such cases may be seen from Pearson's formula for the standard deviation of one variable ( $X$ ) when another ( $A$ ) is constant.

$$A\sigma_X = \sigma_X \sqrt{1 - r_{XA}^2} \quad (3)$$

$$r_{XA}^2 = 1 - \frac{A\sigma_X^2}{\sigma_X^2} \quad (4)$$

The expression  $1 - A\sigma_x^2/\sigma_x^2$  is obviously the portion of the mean square deviation of  $X$  which is directly due to  $A$  if the latter is a cause of variation in  $X$ . In the present case the degree to which pattern is determined by the three independent factors, heredity ( $H$ ), tangible environment ( $E$ ) and irregularity in development ( $D$ ) are measured by  $r_{OH}^2$ ,  $r_{OE}^2$  and  $r_{OD}^2$ . Using the letters of figure 5 for the correlations, we have

$$h^2 + e^2 + d^2 = 1 \quad \text{from (1).} \quad (5)$$

The correlation between parent and offspring is the product of the correlations along the single chain of factors by which they are connected.

$$r_{PO} = hba h = abh^2 \quad (6)$$

The correlation between litter mates is the sum of the products of the correlations along the three connecting paths,

$$r_{OO_1} = habba h + habba h + ee = 2a^2b^2h^2 + e^2. \quad (7)$$

In a sense, the genetic constitution of the fertilized egg is simply the sum of the constitutions of the egg and sperm. The latter are independent

of each other in a population which is mating at random. They are of equal importance, as indicated by the equality of inheritance from sire and dam. The degree of determination in each case must, therefore, be one-half.

$$\begin{aligned} r_{GH}^2 &= a_2 = 1/2 \\ a &= \sqrt{1/2} \end{aligned} \quad (8)$$

The relation between the germ-cells and the genetic constitution of one of the parents is not quite so obvious. It is well known that in a population which is mating at random, the proportion of homozygous and heterozygous classes come to an equilibrium such that the number of those heterozygous in a given factor equals twice the square root of the product of the numbers in the two homozygous classes. For factors  $A$  and  $a$ , the proportion in the three classes can be expressed in the following form:

$$x^2AA + 2xyAa + y^2aa$$

In the production of this population by the preceding generation, there were  $x^2 + y^2$  cases in which similar germ-cells united at fertilization and  $2xy$  cases in which the egg and sperm were dissimilar.

When this population produces germ-cells, there are  $x^2 + y^2$  cases in which gametogenesis results in similar ones, and  $2xy$  cases in which they are dissimilar.

Thus in a population of this kind, the correlation between the germ-cells produced by gametogenesis is exactly the same as that between two germ-cells which unite at fertilization, the correlation in which case, of course, is zero. Consequently, the relation between a germ-cell and the genetic constitution of the parent is the same as its relation to that of the offspring. Thus we may look upon the constitution of the germ-cell as half determined by that of the parent and half by chance at segregation.

$$r_{HG} = b = a = \sqrt{1/2} \quad (9)$$

In considering the genetic constitution of the fertilized egg as simply the sum of the constitutions of the egg and sperm, each heterozygous class is rated as if exactly intermediate between the two corresponding homozygous classes. This is not, however, the correct way to grade the genetic constitution as a factor in development, unless dominance is lacking. The correlation between the two methods of grading depends on the degree of dominance and on the ratio of dominant to recessive factors in the population. For perfect dominance and a distribution of all pairs of allelomorphs according to the proportion  $1AA : 2Aa : 1aa$ , the correlation is  $\sqrt{2/3}$ . The correlation between the genetic constitution of parent and offspring is thus about  $1/3$  if there is perfect dominance, instead of  $1/2$ .

As already noted, the progeny of a cross between two grades of piebald are almost exactly intermediate on the average and the second generation is only slightly more variable than the first. These results might be due to two groups of dominant factors with opposed effects. The most prob-

able explanation, however, is that dominance is lacking and this view will be adopted provisionally.

With this assumption, our three equations for determining the values of  $h^2$ ,  $e^2$  and  $d^2$  are as follows in the two stocks under consideration.

	EXP. B	FAM. 35
(5) $h^2 + e^2 + d^2 = 1$		
(10) from (6), $r_{PO} = 1/2 h^2 =$	0.211	0.014
(11) from (7), $r_{OO1} = 1/2 h^2 + e^2 =$	0.214	0.069
$h^2 =$	0.422	0.028
$e^2 =$	0.003	0.055
$d^2 =$	0.575	0.917
	1.000	1.000

Thus in the control stock, variations in pattern are determined about 42% by heredity, and 58% by irregularity in development, leaving nothing for tangible environmental factors. In the inbred family the corresponding figures are 3% for heredity, 5% for tangible environment and 92% for irregularity in development. We can find the mean squared deviation due to each kind of factor by applying these percentages to the total squared standard deviation of each stock. (Equation 3 and table 1.)

	CONTROL (B)	IMBRED (35)
Heredity, $\sigma_{O,H}^2$ .....	0.271	0.010
Tangible environment, $\sigma_{O,E}^2$ .....	0.002	0.020
Development, $\sigma_{O,D}^2$ .....	0.370	0.334
Total, $\sigma_O^2$ .....	0.643	0.364

If these results had been obtained in the control stock before the inbreeding commenced, the extent to which the variability of the stock should be reduced by inbreeding could have been predicted, assuming dominance to be lacking. Inbreeding automatically renders all Mendelian factors homozygous and, therefore, eliminates all genetic variability. There is no reason for supposing that variability due to environmental or ontogenetic causes would be affected. The sum of the mean square deviations due to the latter causes is 0.372 in the control stock. This, then, is the mean square deviation to be expected after prolonged inbreeding, while its square root, 0.610, is the expected standard deviation. The actual figures in the inbred family, 0.364 for the mean square deviation, 0.603 for the standard deviation, are an even better check than could reasonably be expected on the accuracy of the assumptions on which the degrees of determination were calculated.